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甘肃白垩纪的一个甲虫新科

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摘要 本文记述一种化石甲虫,采自甘肃玉门,白垩纪地层。标本相当完整,虽属中生代产物,却保持有一些较原始的特征,如多节的触角,不平行的鞘翅纵脉,不折的膜翅以及翅端的密集脉纹。据此种种,作者认为鞘翅目应与广翅目近缘,两者源出于共同的原始祖型。

本文所记的甲虫新科玉门蜱科 Umenocoleidae, 系根据一个化石标本,采自甘肃玉门,其岩石地层应为下白垩系。这是一个相当完整的标本,身体背面保存良好,仅头部受损,但是足很不全,只有前足腿节较为清楚。迄今为止,已发现的古生代(二迭纪)和中生代化石甲虫大概已超过五、六百种,但大部分仅有鞘翅,很少这样完整、清晰的标本。尤其值得注意的是这种甲虫还保持有不少的原始特征,它们的组合存在,是任何已知的化石或生存种类所未见的;因此在分类上,我们不得不建立为一个新科,而从系统发育观点,更有其重要意义。

一、分类描述

玉门蜱科 Umenocoleidae, 新科

模式属 *Umenocoleus*, 新属,早白垩世。

描述 体长形。触角丝状,可见十五、六节(图1);下颚须应相当细长,节数不清。前胸宽胜于长,基部远较鞘翅为狭;背板后缘前有一条横沟。鞘翅端部1/3开裂,裂处缝缘扁阔;背面刻点极密,全部混乱;纵脉发达,部分不平行(图3),亚前缘脉(Sc)紧靠前缘(不很清楚),径脉(R)分为两枝,中脉(M)分为四枝,肘脉(Cu)不分枝,臀脉(A)三条彼此紧排。膜翅在鞘翅开裂处外露,不折,密布纵脉(图2)。

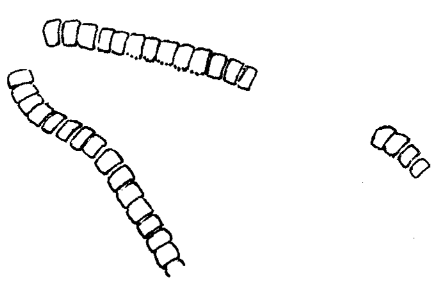

图1 *Umenocoleus sinuatus*, gen. et sp. nov. 触角

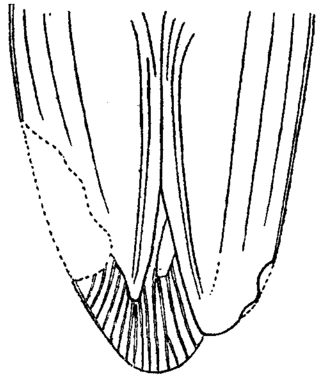

图2 *Umenocoleus sinuatus*, gen. et sp. nov. 身体后半部,示膜翅

系统地位　本新科隶属于鞘翅目 Coleoptera，以其丝状、多节的触角，不折、多脉的膜翅和不平行的鞘翅纵脉等特征组合，和目内所有其他的科相区别。它的亚目地位很难决定；目前一般承认鞘翅目可以划分为三个亚目，即原鞘亚目 Archostemmata，肉食亚目 Adephaga 和多食亚目 Polyphaga；划分的主要根据在于成虫腹面形态、膜翅脉型和幼虫构造，可是我们的化石标本对此都不能有所说明。按可见的特征来分析，新科是一个突出的镶嵌类型，既继承有祖系的原始性状，又有其本系的特殊发展。从原始的一面，本科的开裂式的鞘翅显然和古生代甲虫类似，它的鞘翅脉序，特别是M区（即 R 与 Cu 之间的区域）的扩大和纵脉分枝情况，与二迭纪的 *Kaltanicupes richteri*（隶属于原鞘亚目长扁蜱科 Cupedidae, Родендорф, 1961）可说基本相似（图 4）。从特化的一面，它的前胸构造和鞘翅刻点既和一般古生代甲虫很不相同，也不能归入长扁蜱科；它的整个体形外貌，如果和生存类型比较，看来和多食亚目内的芫菁科 Meloidae、拟天牛科 Oedemeridae 及天牛科 Cerambycidae 的某些种类多少有些相似，但是这种相似性亦可能是一种趋同现象，不能据以断定它和三科之间有近缘关系。因此，关于新科的亚目地位，目前还很难作出判断。

弯脉玉门蜱 *Umenocoleus sinuatus*，新属、新种

（图版 I；图 1—3）

这是新科所依据的唯一的属和种，没有其他的同级类群可作比较，所以这里将不分属种，而合并描述。

产地和层位　一块标本（正模），采自甘肃玉门惠同堡下白垩系灰绿色页岩。采集者：王尚文等（1936. VII. 11）。标本编号：N23，F4704101。标本保存在中国科学院南京地质古生物研究所。

量度　体长（头至后翅末端）17 毫米；前胸长 2.6 毫米，基宽 3.5 毫米；鞘翅长 12 毫米，基部最宽处（两翅并计）6 毫米。

描述　中小型甲虫，头胸栗色，鞘翅棕栗，触角棕红。头部损坏，但可看出其宽度大致与前胸相等；头壳刻点颇密，有似鞘翅，但稍稀；照片（图版 I）上所见的两侧深色斑点在化石上是凹下之处，并非复眼。下颚须仅末节清楚，该节末端钝圆，长达宽的两倍有余。触角不全（图 1），可见十五、六节，估计至少有 20 节，各节宽度大致相等，每节均宽胜于长，近基部数节尤扁而短。

前胸近乎方形，向后稍宽，前缘平直（照片上此缘好象是胸面的一条横沟，实际上这是胸的前部边缘），两侧无边框；盘区十分拱凸，表面粗糙不平，刻点极粗密；后缘前有横沟一条，其两侧向前弯弧，沟后区域不隆，但亦密布刻点。小盾片极小，三角形。

鞘翅基部远较前胸为宽，最宽处在肩部稍后，向端逐渐收狭；每翅基部中区明显隆起，在其后侧的肩瘤似不很发达，两者间有一眉形沟为界，此沟两翅对称，可能不是压损所致；翅面刻点极密，但较前胸为细，全部混乱，刻点间有隆起边缘为界，很少并合。翅脉清晰（除 Sc 较不清楚外），脉序如下（图 3）：Sc 紧靠前缘（分类上称为侧缘），并与之平行；R 在翅基部 1/4 处分为两枝，后枝 Rs 与前枝 R_1 平行，两者伸展到距翅端 1/5 处；M最发达，分为 4 枝，第一、第二两次分枝均在 R 分枝之前，M_1 与 Rs 平行，其余 3 枝均向后弧弯，在翅中部占全翅面积之半；Cu 从翅基部隆起的中区，斜伸至后缘（即缝缘）中部稍前；A 共三条，

彼此紧排，A_1 最长，约为翅长的 1/3[1]。

膜翅端部外露，由于鞘翅开裂，而且左边的鞘翅端部缺失，可以清楚看到此虫的膜翅并不折合于鞘翅之内，而且密布纵脉（图 2），和现今生存的甲虫膜翅迥不相同。

足几乎全部损坏，仅隐约可见前足腿节，相当粗壮。

二、讨 论

鞘翅目是动物界最大的目，已知的生存种类约有 27 万，一般估计动物界已知有 100 万种，鞘翅目的种类超过动物全部的四分之一，占着很大的数量优势。可是我们对于这个重要大目的发展历史，它的起源与进化过程却还很少知道。化石资料在这方面亦很少明确的指示。最早的鞘翅目化石纪录见于古生代二迭纪，这时的类型虽较原始，但已相当复杂，已发现的将近 100 个种可以归纳为十来个不同的科（Родендорф, 1961），其中绝大部分均已灭绝，仅一个科生存至今，即原鞘亚目的长扁岬科。中生代的甲虫资料较多，分析这些资料，可见有两点颇堪注意：第一，区系的性质已呈现近代面貌，不若二迭纪之具有鲜明的原始特点，因而所描述的种类很多地位可疑，既与近代类型接近，又不能归入近代科别（标本残碎也是科别难定的一个重要原因）。第二，各纪的资料分布很不均匀，较早的三迭纪、侏罗纪远远较多，较后的白垩纪反而较少。据 Handlirsch（1939）统计，在已知的数百种中生代甲虫中，属于白垩纪的仅 21 种。基于这些情况，玉门岬科的发现是颇有意义的，它不仅是属于稀见的白垩纪区系成份，更重要的是，它所呈现的原始性状是一般中生代甲虫所未见的，某些性状甚至是古生代甲虫所未见的。这些原始性状可以帮助我们探索甲虫的早期面貌和进化渊源，特别是联系到鞘翅目与广翅目近缘的学说，可以提供一些线索和支持。

玉门岬的原始特征表现在以下几个方面：

1. 多节的丝状触角（图 1） 现代甲虫的触角一般是 11 节，有的较少，很少较多。古生代甲虫化石尚未发现有完整的、11 节以上的触角；中生代侏罗系地层曾发现有完整的甲虫触角，亦是 11 节。但是玉门岬的触角肯定是多节的，化石上两个触角都有，只是节数不全，上面的触角可见十二、三节，在其右方较远处还有脱离的三、四节（照片上未摄入），下面的触角亦可见有十五、六节；从两个触角的地位来推想，每一触角至少应有 20 节。昆虫触角的总的演化趋势是从多节到寡节，较原始的有翅昆虫（如蜚蠊目、蜉蝣目、古网翅目等）和较原始的全变态类（如脉翅目、长翅目等）的触角都是多节的。因此，我们推想玉门岬的多节触角，正如它的不平行的鞘翅脉序一样，很可能是一种原始性状；在鞘翅目内，触角演化的总趋势是从多节到寡节的。

2. 开裂式的鞘翅 古生代甲虫化石虽极大部分是单个的鞘翅，但从其端部两边收狭或缝端明显弯弧的形状，可以说明它是属于开裂式的。Sojanocoleidae 科、Permorrhaphidae 科、Permosynidae 科、长扁岬科以及和长扁岬近缘的许多种属，都是如此（图 4, 5），只有 Tshekardocoleidae 科较不显著。我们有理由设想，开裂式的鞘翅是甲虫的一种原始性状，玉门岬保持了这种性状。

1) 从化石标本，我们不能看到各脉在翅基沿的分枝情况，只能从可见的基部分枝关系和分布情况作为鉴定根据，因而所定的脉纹名称，可能会有不同意见。

开裂式鞘翅亦散见于现代甲虫的不同类群，如多食亚目内异跗类（Heteromera）的芫菁科、伪天牛科及大花蚤科（Rhipiphoridae）等都有这种情况。可是在这些科内，由于其整个体形构造很少保持原始特征，更由于其许多近缘的较原始类群的鞘翅在缝缘全部嵌合，说明这种开裂是一种特化现象，正象有翅亚纲内的失翅现象一样，是次后获得的。

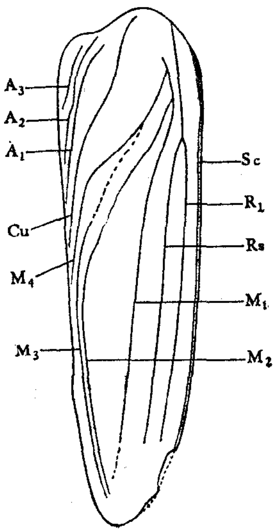

图 3 *Umenocoleus sinuatus*, gen. et sp. nov. 右鞘翅

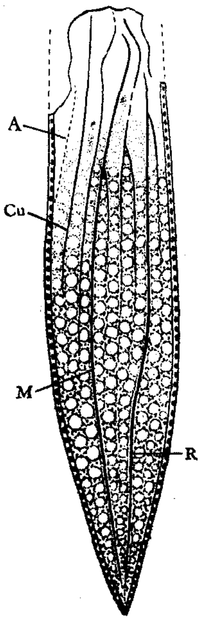

图 4 *Kaltanicupes richteri* Rohd. 右鞘翅（据 Rohdendorf, 1961）

3. 不平行的鞘翅纵脉（图 3）这是玉门岬的一种最显著的原始特征。我们知道，昆虫的膜翅翅脉一般都不是纵直平行的，所以甲虫的前翅在未特化为鞘翅之前，其翅脉亦该是不平行的，即使在形成为鞘翅之后，翅脉的纵直平行化亦并不是立即实现，而是逐渐发展的。在整个鞘翅目内，包括所有已知的化石和生存类群，如果从翅脉的平行化程度来判断，可以把鞘翅脉相归纳为三个主要类型：（1）仅前缘脉纹（Sc 和 R）纵直平行，如玉门岬；（2）前缘和后缘（Cu 和 A）脉纹纵直平行，仅中脉（M）不平行，如 *Sojanocoleus*（图 5）；（3）全部主脉，包括中脉在内，均呈纵直平行，如一般甲虫。这三个类型大致可以代表翅脉平行化的三个不同阶段，其过程为：前缘脉纹最先平行化，其次是后缘脉纹，最后是中脉。

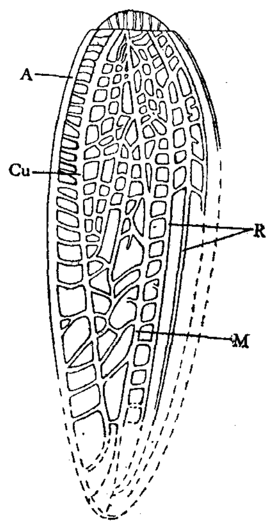

图 5 *Sojanocoleus reticulatus* Martynov（据 Martynov, 1932）

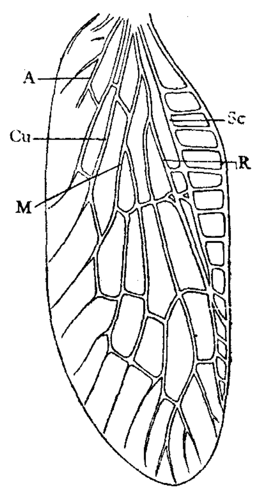

图 6 *Sialis* (Megaloptera) 前翅（据 Richter, 1935）

玉门岬的鞘翅脉相属于第一类型，因而是目前所知的最原始类型。和古生代甲虫比较，它和长扁岬科 *Kaltanicupes* 属的脉相（图 4）最近似，后者的M亦很发达，分为四枝，Cu 与 A 亦相对较短，斜伸向翅后缘；但是玉门岬的M更为弧弯，A更为齐全，因而更为原始。

把这个原始类型和广翅目的前翅脉序比较，可以得到更有意义的启示。我们看到，两种脉序的相似性是非常显著的：以 *Sialis*（图 6）为例，它的 R 与 Rs 如果除去支枝，即与玉门岬十分相似；M脉端部亦有四个

主要支枝，只是分枝较后，差异较大；但是斜短的 Cu 与三条平行的 A，两者又基本相同；所以总起来讲，两种脉序显然系属于同一基本类型。Richter (1935) 曾把 *Sojanocoleus* 和 *Sialis* 比较，注意到两者之间的相似性，而玉门蜱在这方面更为显著。目前不少甲虫学者，根据现代幼虫的比较形态学研究，从广翅目的 *Sialis* 型或 *Raphidia* 型幼虫与甲虫幼虫比较，认为两者具有密切的亲缘关系，鞘翅目应起源于广翅目 (Théodoridès, 1952)。玉门蜱的鞘翅脉序可给这个学说以一定的支持，只是我们认为两个目之间的关系不一定是直系的，即鞘翅目不一定是广翅目的直系后代，更可能是同一祖系的近缘分支。

但是玉门蜱的鞘翅脉序亦有其明显特化的一面，它没有横脉，更没有象 *Tshekardocoleus*、*Permocupes*、*Permocupoides*、*Sojanocoleus* 等属所保持的那种古老网脉，这类脉纹在玉门蜱都已经是消失了，没有留下痕迹。

4. 不折迭的膜翅（图 2） 很难肯定这是否原始特征。古生代的甲虫化石标本未见膜翅，仅 *Archicupes reichardti* 在鞘端开裂处略露膜翅，从 Родендорф (1961) 的插图看来虽似折迭，但不能十分肯定。中生代有少数化石标本显露膜翅，以侏罗纪的 *Ditomoptera dubia* 最完整，观察 Handlirsch (1906—08) 的图，可见这个种的膜翅虽然没有清楚折痕，但从图上鞘翅张开、膜翅伸出腹部很远的情况，可以断定其在休止状态下是折迭的。现代甲虫的膜翅都折迭于鞘翅之下，只有少数例外，如大花蚤科 (Rhipiphoridae) 和筒蠹科 (Lymexylonidae) 的短鞘种类，其鞘翅呈残留状态，膜翅均外露不折。这个不折显然是一种后起特征，是随着鞘翅短缩而演变的特征，因为同科内所有的长鞘种类亦都是折迭的；而筒蠹科则因鞘翅和腹部特别长，因而膜翅折迭型式与一般不同。但大花蚤科的情况，最富说明意义：这个科内有很多种类和玉门蜱一样，鞘翅呈开裂式，可是其膜翅折迭情况却和一般甲虫完全相同；这充分说明了该科内短鞘种类之膜翅不折，是一种后起的特征。

基于上面的许多事实，玉门蜱的膜翅不折状态，特别引起了我们的注意。不论从照片上或化石标本上都可看到（照片上的纵折是左面鞘翅的界纹，不是膜翅之间的交迭界纹），它所露出的膜翅，地位是完全正常的，肯定是自然的休止状态；然而它的开裂式的鞘翅，如前所述，又可肯定其为原始现象，不是后起的减缩现象。因此，我们可以作出这样的推想，即玉门蜱的不折的膜翅，和现代甲虫所见的不同，是从祖先所继承的一种原始特征。据此推想，在鞘翅目的进化过程中，首先应是前翅特化为鞘翅，由于这种特化，飞行的功能不得不主要由后翅来负担，然后随着进化的前进，后翅逐渐发展而演变为鞘下折迭；演变为折迭以后，某些种类又随着鞘翅的减缩，再度演变为不折。

玉门蜱膜翅的另一个重要特点是端部密布纵脉，这亦该是一种较原始的特征。图 2 显示了这个部分的纵脉分布情况，它和全变态类中较原始的广翅目及脉翅目脉序很相类似，因而对于鞘翅目与广翅目近缘的学说，提供了又一种有意义的根据。

综上所述，我们探讨玉门蜱的原始特征，联系到鞘翅目的系统渊源，可以得到如下的两点推想：

第一，鞘翅目的原始类型应具有以下的几项特征：(1) 触角呈多节式；(2) 鞘翅呈开裂式；(3) 鞘翅纵脉大部分不纵直平行，以 M 最发达；(4) 膜翅在休止时不折迭。

第二，鞘翅目与广翅目最近缘，两者应是同一祖系的分支发展，玉门蜱的鞘翅和膜翅

脉序,给予这个见解以古生物学上的支持。

参 考 文 献

Родендорф, Б. Б. 1961 Палеозойские Насекомые Кузнецкого Бассейна. Тр. Палеонт. ин-та АН СССР, Т. 85. стр. 393—468.

Handlirsch, A. 1908 Die fossilen Insekten und die Phylogenie der rezenten Formen. Leipzig.

——————, 1939 Neue Untersuchungen über die fossilen Insekten. Teil II. Ann. Naturh. Mus. Wien., Bd. 49, SS. 12—169.

Richter, A. A. 1935 On the elytral venation of Coleoptera. *Rev. d'Ent. URSS* **26**:25—58.

Théodoridès, J., 1952 Les Coléoptères fossiles. *Ann. Soc. Ent. France* **121**:23—48.

外 文 摘 要

A NEW FAMILY OF COLEOPTERA FROM THE LOWER CRETACEOUS OF KANSU

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The new beetle family, Umenocoleidae, described in this paper is based on a single fossil specimen, collected from the greenish-gray shale of the Lower Cretaceous of Yumen, Kansu. This is a quite complete specimen with the dorsal part of body well-preserved, only the head being damaged. Among the Palaeozoic and Mesozoic beetles so far discovered, none had been so completely and distinctly preserved. Particularly noteworthy is the fact that it presents a combination of archaic features which may afford useful data in the discussion of the problem concerning the origin of Coleoptera.

I. Systematic Description

Umenocoleidae, fam. nov.

Type genus: *Umenocoleus,* gen. nov., Lower Cretaceous.

Description: Body elongate. Antennae filiform, with 15—16 visible segments (Fig. 1). Pronotum slightly broader than long, transversely grooved before the base. Elytra much broader at base than prothorax, dehiscent at apical third where the sutural margins are broadened and flattened; disc very densely and confusedly covered with punctures; longitudinal veins well-developed (Fig. 3), partly non-parallel, Sc close to anterior margin (less distinct), R composed of two branches and M four branches, well-developed; Cu represented by a single vein and A three veins, closely arranged. Membranous wings exposed at apex between the dehiscent elytra, non-folded, densely distributed with longitudinal veins (Fig. 2).

This new family may easily be distinguished from all the other known families of Coleoptera by a combination of the following characters: the filiform and multi-segmented antennae, the non-folded and multi-venous membranous wings and the dehiscent elytra, with the medial veins well-developed and non-parallel. Its suborder position is hard to determine, as the characters on which the suborders of Coleoptera are based,

such as the morphology of abdomen, the venation of hind wings and the structure of larvae, are not available in our fossil specimen.

The beetle is eminently mosaic in nature; it is a complex of primitive and specialized features. As we shall see in the following pages, its multi-segmented antennae and non-parallel elytral venation are certainly primitive features, while its pronotal structure and elytral punctuation are much specialized, being very different from those of the generalized form of the Palaeozoic Era. In general physiognomy, the new fossil resembles certain existing species of the families Meloidae, Oedemeridae or Cerambycidae, but the resemblance may likely be a phenomenon of convergence and not an indication of true relationship. Hence the present beetle, as the type of a new family, is so characteristic and remarkable in spite of the fact that its suborder position can hardly be ascertained.

Umenocoleus sinuatus, gen. et sp. nov.

(Plate I. Text figs. 1—3)

Locality and horizon: A single specimen, no. N23, F4704101 (holotype), collected from Hui-ton-bou, Yumen, Kansu, by Wang Shang-wen (July, 11, 1936), in the greenish-gray shale of Lower Cretaceous. Deposited in the Nanking Institute of Geology and Palaeontology, Academia Sinica.

Measurements: Body length (from head to tip of hind wing), 17 mm.; width (humeral region of elytra), 6 mm. Pronotum length, 2.6 mm.; width (basal part), 3.5 mm. Elytron length, 12 mm.

Description: Beetle of medium size, head and pronotum castaneous, elytra castaneous-brown, antennae red-brown. Head incomplete, appearing as broad as pronotum, densely punctate. Maxillary palpi with only the last segments distinct, which is elongate with apex broadly rounded. Antennae incomplete, with 15—16 visible segments, more or less equal in size, each slightly broader than long, the basal ones somewhat shorter.

Pronotum subquadrate, broadened behind, sides unmargined, anterior margin straight (appearing in photo like a transverse furrow of the disc); disc rather strongly convex, coarsely, rugously and densely punctate; in front of the base, there is a transverse furrow which is arching forward at sides; behind the furrow, the area is not raised but densely punctate. Scutellum small, triangular.

Elytra much broader at base than pronotum, broadest slightly behind the shoulder and gradually narrowed toward apex; humeral calli not quite well-developed, median basal area of each elytron distinctly raised and separated from the callus by a brow-like furrow; surface very densely and confusedly punctate, the punctures finer than those of pronotum. Veins well-developed and distinct (Fig. 3): Sc close and parallel to anterior margin (less distinct); R branching into two from the basal fourth, R_1 and Rs, the two parallel, both extending to about the apical fifth of the elytron; M very well-developed, with four branches, both the primary and secondary branchings taking place before the branching of R; M_1 parallel to Rs, M_2-M_4 arching backward, the four branches occupying about half the area of the elytron medially; Cu extending obliquely from the raised basal median area to a little before the middle of the posterior margin (or sutural margin); A consisting of three branches, closely arranged,

A_1 being the longest, about one-third the length of the elytron.

Membranous wings naturally unfolded, densely distributed with longitudinal veins, being thus very different from the present-day beetles.

Legs not seen, except a fairly stout anterior femur which is barely visible.

II. Discussion

The Coleoptera form the largest order in the animal kingdom, about 270,000 existent species having already been described. But in such a large and important order, very little is known about its origin and evolution. The earliest known fossil beetles date from the Permian period. A fairly rich material has recently been accumulated (Rohdendorf, 1961), showing that a variety of forms had already existed at that remote time, but their phylogenetic history is far from being clear. The discovery of *Umenocoleus* is, therefore, of great interest, as it presents a number of archaic features, some of which have hitherto been unknown to the Mesozoic or even Palaeozoic forms. Such archaic features may help us to trace the early features and evolutionary history of the order, particularly in considering the current theory of the close relationship between Coleoptera and Megaloptera.

The archaic features of *Umenocoleus* are as follows:

1. Multi-segmented antennae: The antennae of the present-day beetles are generally 11-segmented, rarely less or more. In Mesozoic beetles, those discovered with antennae complete are found to possess 11-segmented antennae. In Palaeozoic beetles, there has not yet been found any complete antenna of over 11 segments. But the antennae of *Umenocoleus* are distinctly multi-segmented. They are incomplete, from what can be seen (Fig. 1), the upper one with 12 or 13 segments and 3 or 4 dislocated ones at its right side (not seen in the photo), the lower one with 15—16 segments. Judging from the position of the antennae, it is estimated that each of them should have at least 20 segments. As the general trend of evolution of the antennae in insects is from multi-segmentation to pauci-segmentation, we may reasonably presume that the multi-segmented antenna of *Umenocoleus* is most likely a primitive character.

2. Dehiscent elytra: In the Palaeozoic fossil beetles, such as Sojanocoleidae, Permorrhaphidae, Permosynidae, Cupedidae and species related to Cupedidae, the elytra are always more or less fusiform and dehiscent at apex. Hence, it seems very probable that the dehiscent type of elytra represents a primitive feature of Coleoptera, characterizing a primitive stage in the evolution of beetles, at which the two elytra have not yet been perfectly fitted to each other at their resting condition. *Umenocoleus* apparently retained this primitive structure.

The dehiscent type of elytra is also found in certain existing groups of beetles, such as in Meloidae, Oedemeridae and Rhipiphoridae. But here, dehiscence appears to be secondarily acquired, similarly as apterism in Pterygota.

3. Non-parallel elytral veins: This is the most conspicuous feature of primitiveness in *Umenocoleus*. The anterior wings of beetles, before they became specialized into elytra, should have their longitudinal veins non-parallelly arranged as those of hind wings, and in the course of specialization, the straightening and parallelization of veins would have been gradually realized. Thus, by comparing the elytral venation in the various groups of beetles, both living and extinct, we may distinguish three

principal types which seem to represent roughly the three different stages of specialization. In the first type or stage, the anterior veins (Sc and R) only are straightened and parallelly arranged (*e. g., Umenocoleus*); in the second, the posterior veins (Cu and A) also become straightened and parallel (*e. g., Sojanocoleus*, Fig. 5); in the third, the medial veins (M) are finally specialized, thus completing the straightening and parallelization of the veins (*e. g.*, present-day beetles).

The venation of *Umenocoleus* belongs to the first type. It is, therefore, the most primitive. Among the Palaeozoic beetles, only the Cupedid genus *Kaltanicupes* exhibits a similar type of venation (Fig. 4), with M well-developed and four-branched, and Cu and A short and oblique. But in *Umenocoleus*, M appears to be more arcuate, A more complete, being thus more primitive than *Kaltanicupes*.

One could gain an insight of much significance by comparing this primitive type of venation with that of Megaloptera, for instance, with *Sialis* (Fig. 6). If discounting the branches of R and Rs of the latter, we may readily realize that their venations are fundamentally the same, only in the latter, the branching of M taking place somewhat more posteriorly. Richter (1935) had compared *Sojanocoleus* and *Sialis* and noticed their similarity, but the similarity between *Umenocoleus* and *Sialis* appears to be even more striking. Hence, the elytral venation of *Umenocoleus* may be considered as a further evidence to the theory of deriving Coleoptera from Megaloptera, the assumption being originally based on comparative studies of larval morphology. We are, however, of the opinion that Coleoptera may not be direct descendants of Megaloptera; they are more likely two closely related branches of a common ancestor.

The elytral venation of *Umenocoleus* has also its specialized feature, that is, without cross veins, especially without such archedictyon as those found in the Palaeozoic genera, *Tshekardocoleus, Permocupes, Permocupoides* and *Sojanocoleus*.

4. Non-folded membranous wings: It is an important character of Coleoptera that the membranous wings are always folded up under the elytra in their resting condition. Exceptions are found only in some groups with strongly reduced elytra, but in these groups, the non-folded condition is obviously a secondarily acquired feature, resulting from a shortening of the elytra, as their related groups with long elytra do possess folded membranous wings.

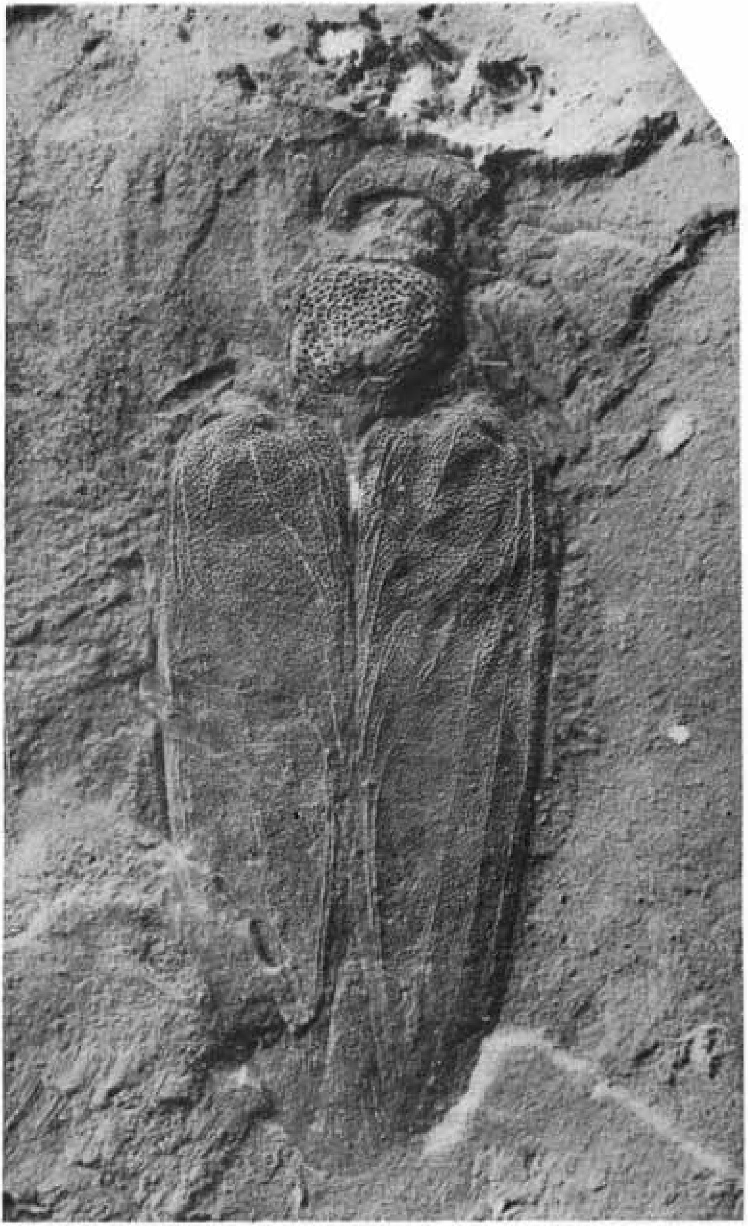
In view of the above mentioned facts, the non-folding of the membranous wings of *Umenocoleus* is a feature of special interest. Either from photo or fossil (the longitudinal fold shown on the photo is the inner margin of the left elytron, not the demarcation between the overlapping wings), we can clearly see that the exposed membranous wings are in their natural resting condition. Since the dehiscence of elytra in this beetle is a primitive character, not a secondary one, we must consider the non-folded membranous wings of *Umenocoleus* as an archaic feature.

Another important feature of the wings of this beetle is that they are densely distributed with longitudinal veins at apex. This should also be considered as an indication of primitiveness. The venation thus bears a strong resemblance to that of the primitive Holometabola of the orders Neuroptera and Megaloptera—a fact by which is again evidenced a close relationship between Coleoptera and Megaloptera.

To sum up, in discussing the archaic features of *Umenocoleus*, we are led to draw the two following deductions:

First, that the primitive Coleoptera would possess the following characters: 1. antennae multi-segmented; 2. elytra dehiscent; 3. longitudinal veins of elytra mostly non-parallel, with M well-developed; 4. membranous wings not folded in their resting condition.

Secondly, that Coleoptera and Megaloptera are closely related groups, having been originated from a common ancestor, but developing into two different branches. The venation of both elytra and membranous wings of *Umenocoleus* afford a palaeontological support to this view.



弯脉玉门鞘 *Umenocoleus sinuatus*, gen. et sp. nov. 背视，×8